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MANDIBULAR MORPHOLOGY OF THE MID-MIOCENE SEAL *DEVINOPHOCA CLAYTONI* (CARNIVORA, PHOCIDAE, DEVINOPHOCINAE)

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Mandibular Morphology of the Mid-Miocene Seal *Devinophoca claytoni* (Carnivora, Phocidae, Devinophocinae). Rahmat, S. J., Koretsky, I. A. — During several excavations in Slovakia at the base of the Malé Karpaty Mountains (near the junction of the Morava and Danube Rivers), two skulls and numerous mandibular, dental and postcranial bones of early mid-Miocene (16.3–12.8 Ma) seals were collected. Isolated mandibles and many individual teeth were found at this locality, with some teeth in situ corresponding morphologically with the mandible and skull of *Devinophoca claytoni*, and others perfectly associating to the mandible and skull of the recently described *Devinophoca emryi*. Based on this material, two species of the previously unknown phocid subfamily Devinophocinae Koretsky et Holec, 2002 have been described. However, the mandibular morphology of the type species *Devinophoca claytoni* has remained unknown. Here, we present a first description of the mandible of this species. Morphological assessments reveal that the *D. claytoni* mandible has posterior alveoli larger than anterior; flat mandibular body low in height; alveoli of p4 larger than m1; and a unique devinophocine combination of incisors (I3/1) that differs from those in the extant subfamilies Cystophorinae (I2/1), Monachinae (I2/2) and Phocinae (I3/2).

Key words: Phocidae, *Devinophoca*, Miocene, Badenian, Central Europe, Vienna Basin.

Introduction

The classification of phocids (true seals) remains very controversial (Koretsky and Rahmat, 2013), as the Family Phocidae has been considered monotypic (Sokolov, 1979; Wyss, 1987; Wozencraft, 1989; McKenna and Bell, 1997) or separated into the subfamilies Monachinae and Phocinae (Burns and Fay, 1970; Muizon, 1992; King, 1983; Wyss, 1994; Berta and Sumich, 1999; Árnason et al., 2006; Berta et al., 2015). Most molecular studies support division of true seals into two subfamilies, but they do not take into account important morphological characters and the fossil record (Koretsky et al., 2016). We maintain that studies classifying seal taxa must incorporate morphology and the fossil record to be more accurate.

On the other hand, there is no consensus from morphological studies. The Berta and Wyss (1994) study presented phocids as members of a clade that includes walruses, allodesmines, and desmatophocines, groups that traditionally had been regarded as close to otariids (Repenning and Tedford, 1977; Yonezawa et al., 2009;

Churchill et al., 2014) or, in fact, as being otariids (Mitchell, 1968). Barnes and Hirota (1994:355) showed that the seven characters that Berta and Wyss (1994: 41–42) interpreted as uniting Allodesminae (and other Otarioidea) with Phocidae were unreliable. The detailed morphology and discussion of the “pinniped” flipper structure was presented by Bininda-Emonds and Russell (1996), who reached a conclusion opposite to Wyss (1994), demonstrating additional support to a likely diphyletic origin. Several of the features discussed in the Koretsky et al. (2016) publication directly supported the Bininda-Emonds and Russell (1996) study.

Some distinctive morphological characters of the skull and mandible can be used to place seals into their respective subfamilies (table 1). Molecular studies use only living taxa and disregard character states for fossil members of living and extinct clades, a noteworthy deficiency that cannot be ignored. Incorporating fossil and extant morphological characters is critical to generate ancestral reconstructions and correctly determine the distribution of characters in the entire evolutionary history of a clade (Koretsky et al., 2016). Molecular studies demonstrate that odobenids is more closely allied with otariids than with phocids (agreeing with the majority of morphological and molecular evidence) and that there is a basal split between Phocidae and an Odobenidae-Otariidae clade (Flynn et al., 2005; Árnason et al., 2006; Fulton and Strobeck, 2006). Different molecular studies on the phylogenetic relationships within Phocidae show numerous variations (Nyakatura and Bininda-Emonds, 2012), with molecular data sets creating an unresolved relationship between Ursidae, Pinnipedia and Musteloidea (Árnason et al., 2006). The Árnason et al. (2006) study determined that early otarioid and otariid divergences occurred in the North Pacific, while phocids began in the coastal areas of the North Atlantic and then dispersed to colder environments. The fossil record does not support a North American origin of phocids, as paleontological evidence shows a North Atlantic origin of phocids in the Paratethyan/Mediterranean regions and an east to west distribution (Koretsky and Holec, 2002; Koretsky and Barnes, 2006; Koretsky et al., 2012; Koretsky and Rahmat, 2013, 2015; Koretsky and Domning, 2014; Koretsky et al., 2015). Although molecular studies are currently accepted as the best type of analysis for classification of seals, it is clear that controversy still exists and there are significant differences in resulting phylogenetic relationships.

Ideally, molecular and morphological analyses should be performed together such as in Scheel et al. (2014), whose results erected a new genus (*Neomonachus*) by combining the Caribbean and Hawaiian monk seals together. The phylogenetic analyses by Koretsky (2001), Koretsky and Holec (2002) and Koretsky and Rahmat (2013) support the division of the family Phocidae into one extinct subfamily (Devinophocinae; Koretsky and Holec, 2002; Koretsky et al., 2016) and three extant subfamilies (Cystophorinae, Monachinae and Phocinae; Koretsky and Rahmat, 2013). It is important to note that even some morphological studies choose to ignore important incomplete fossil postcranial bones and cranial material that is aged older than the scope of their study.

During excavations at the Bonanza site, located near the junction of the Morava and Danube Rivers (Koretsky and Rahmat, 2015; fig. 1) at the base of the Malé Karpaty Mountains in Slovakia, a single skull and numerous mandibular, dental and postcranial bones were collected, in close proximity to each other (approximately 2 m apart). Previous studies have described numerous vertebrate fossil material from this site (Holec et al., 1987; Holec and Sabol, 1996; Holec et al., 1997; Schultz, 2004; Fejfar and Sabol, 2009).

In our description of a new species (*Devinophoca emryi*) of the extinct phocid subfamily Devinophocinae (Koretsky and Rahmat, 2015) from the early Badenian, early middle Miocene (16.3–12.8 Ma), we demonstrated that the *Devinophoca* material (skull, mandibles and teeth) presents mixed characters with the three extant phocid subfamilies (Cystophorinae, Monachinae and Phocinae) as well as specific, distinctive characters.

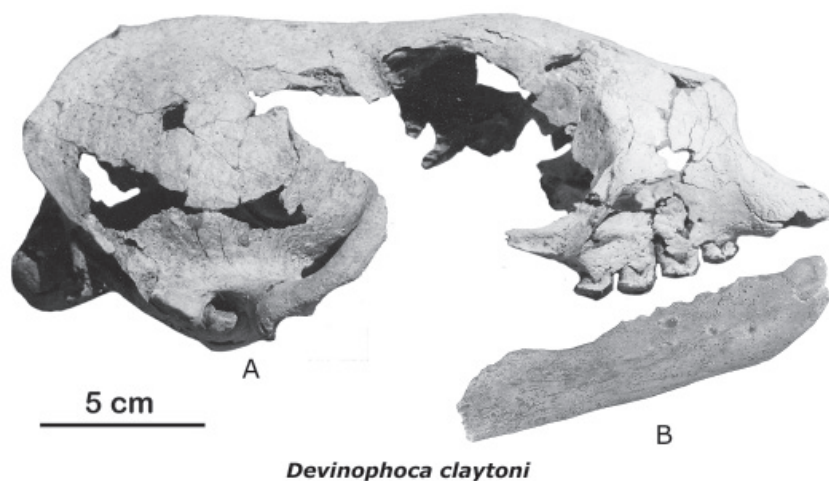


Fig. 1. *Devinophoca claytoni* A — incomplete skull with right M1 and left P2-M1 (Z14532, holotype) and B — left mandible without ramus (SNMZ 25510; referred material) from the Museum of Natural History, Slovak National Museum, Bratislava, Slovak Republic.

Koretsky and Rahmat (2015) detailed morphological associations of discovered mandibles with the skulls of *D. emryi* and *D. claytoni*, all found in close proximity to each other in the same locality. Koretsky's (2001) ecomorphotype analysis, associating the mandible with the humerus and femur based on the morphology of individual, isolated bones and the ecology of living species, demonstrate associations between mandibular and postcranial material. This methodology confirmed that postcranial bones found at the Bonanza site do belong to *D. emryi* (Rahmat and Koretsky, 2016). Numerous other authors (Muizon, 1981 b; Koretsky and Grigorescu, 2002; Goldin and Pilipenko, 2012; and Amson and Muizon, 2014) use associated parts of the skeleton (some complete and others incomplete) to help correlate isolated bones. The ecomorphotype analysis in seals is not unique and is further supported by the division of phylogenetically unrelated taxa using ecological and morphological characters. This type of morphological and ecological association has also been demonstrated in other groups of vertebrates, such as rabbits (Ge et al., 2013), finches (Bowman, 1961) and lizards (Losos, 2011).

The skull and partial mandible of *D. claytoni* are well preserved and the size, dimensions and orientation of this mandible directly associate with the previously described skull of *D. claytoni* (fig. 1; Koretsky and Holec, 2002). Morphology of *D. emryi* maxillary and mandibular dentition described previously (Koretsky and Rahmat, 2015) shows direct association with the *D. emryi* skull and mandibles. Likewise, mandibular dentition of *D. claytoni* associates with the *D. claytoni* skull only.

In this study, we describe the first mandible known of *Devinophoca claytoni* from Bonanza and compare it with that of *D. emryi* and with representative mandibles of other phocid subfamilies to increase the knowledge of the devinophocine morphology. Material was collected by team-members from the U.S., Slovakia and Ukraine at the same site and age as material for its sister taxon, *D. emryi*. As demonstrated in Koretsky and Rahmat (2015), several isolated mandibles and many individual teeth were found at the Bonanza locality, with some teeth in situ corresponding morphologically with the mandible and skull of *D. claytoni*, while others associate perfectly in situ to the mandible and skull of *D. emryi*.

Overall, *D. claytoni* shares mixed characters with the three extant phocid subfamilies as well as presents distinguishing traits not previously described, similar to *D. emryi* (Koretsky and Rahmat, 2015; Rahmat and Koretsky, 2016). Members of the subfamily Devinophocinae demonstrate the most primitive characters known to date, making this subfamily the possible ancestral morphotype for all seals.

Abbreviations: **SNMZ**, Department of Paleontology, Slovakian National Museum, Bratislava, Slovak Republic; **USNM**, National Museum of Natural History, Smithsonian Institution, Washington, D.C., USA.

Systematic Paleontology

Order CARNIVORA Bowdich, 1821

Superfamily PHOCOIDEA Gray, 1825

Family PHOCIDAE Gray, 1825

Subfamily Devinophocinae Koretsky & Holec, 2002

Genus *Devinophoca* Koretsky & Holec, 2002

Type species: *Devinophoca claytoni*

Type locality: Stockerau lime plant, Bonanza Devínska Kobyla, outskirts of Bratislava, Slovak Republic.

Distribution: early Badenian (MN 6), early middle Miocene (16.3–12.8 Ma); Central Paratethys, Vienna Basin of Western Slovakia.

Included species: *D. emryi* and *D. claytoni*

Emended diagnosis: Mandibular body low in height (as in Monachinae and Phocinae); symphyseal part of mandible thick and straight (similar to Monachinae); diastemata between teeth absent (as opposed to Cystophorinae, Monachinae and Phocinae); unique incisor combination I3/1 (as opposed to Cystophorinae, Monachinae and Phocinae); p4 alveolar width and length greater than those of m1 (similar to some Monachinae and Phocinae).

Devinophoca claytoni Koretsky & Holec, 2002 (figs 1–3; tables 1–2)

Referred material: SNMZ 25510, Incomplete left mandible missing ramus and most teeth.

Range: Badenian, early middle Miocene (16.3–12.8 Ma; Wagerich et al., 2014); Central Paratethys, Vienna Basin of Western Slovakia.

Amended diagnosis: Body of mandible low in height (12 mm) and retromandibular (length ~19 mm) region flat (similar to *D. emryi*), with long, wide and round alveoli; mental process not present as opposed to *D. emryi*, but located between p1 and p2; symphyseal part pronounced, symphysis reaches anterior alveolus of p2 (similar to *D. emryi*); p3–m1 tooth row oriented parallel to mandibular axis (similar to *D. emryi*); p4 alveoli wider and longer than those of m1 (similar to *D. emryi*); m1 single rooted (as opposed to *D. emryi*, with fused double-rooted m1); p2 and canine oriented obliquely to mandibular axis (as opposed to *D. emryi*); one lower incisor (as in *D. emryi*); diastemata absent (similar to *D. emryi*).

Description and comparison to *Devinophoca emryi*

While the complete description of the *Devinophoca claytoni* skull has been detailed by Koretsky and Holec (2002), this is the first description of a mandible assigned to this species. The canine is present, but the remaining teeth have fallen out. The mandible lacks the upper portions of the mandibular ramus including the condyloid and coronoid processes (fig. 1; table 1).

The *Devinophoca claytoni* mandible (fig. 2, A–C) has only one incisor, one canine, four premolars and one molar, similar to the dental formula of *D. emryi* (Koretsky and Rahmat, 2015) and other Phocidae. *D. claytoni* and *D. emryi* (fig. 2, D–F) share a unique combination of incisors (I3/1) that differ from all known fossil and Recent Cystophorinae (I2/1), Monachinae (I2/2) and Phocinae (I3/2). The *D. claytoni* p1 alveolus is single-rooted and is compressed craniocaudally. The p2 alveoli are round and not equal in size. The posterior alveoli of p2–p4 are much smaller than their anterior alveoli. The p2–p4 alveoli are double-rooted and m1 is single-rooted, while in *D. emryi* p2–m1 are all double-rooted. The anterior alveolus of p3 is significantly larger than the posterior alveolus. The p3 posterior alveolus is round and the anterior alveolus is compressed craniocaudally. The anterior alveolus of p4 is larger than the posterior alveolus and both alveoli are compressed craniocaudally. The alveolar width and length of p4 is greater than m1, similar to *D. emryi*. The alveolus of m1 is compressed craniocaudally and is single rooted, a rare character (fig. 2, C). *D. emryi* has a fused double-rooted m1 that may appear single-rooted in the occlusal view of fig. 2, F. However, morphological examination of these mandibles clearly shows a single, rounded m1 alveolus for *D. claytoni* and an alveolus in *D. emryi* that is oval shaped with a slight division within, demonstrating a fused, double-rooted m1. According to the study by Boessenecker and Churchill (2016) and our observations from the Smithsonian comparative collection, *Mirounga leonina* m1 roots are variable, with some single rooted and others double-rooted.

The body of the *D. claytoni* mandible is low in height, similar to *Devinophoca emryi*,

Table 1. Some diagnostic skull and mandibular characters separating the four subfamilies of seals

Characters		Cystophorinae	Devinophocinae	Monachinae	Phocinae
Skull	Number of Incisors	6 incisors; 2/1	8 incisors; 3/1	8 incisors; 2/2	10 incisors; 3/2
	Anterior Palatal Foramen	Oval and shallow	Oval and deep	Tend to disappear	Well developed, with a groove
	Interorbital width	Less than 30 % but equal to or greater than 25 % of mastoid width (widened)	Less than 30% but equal to or greater than 25% of mastoid width (widened)	Less widened than Cystophorinae and Devinophocinae	Narrow
	Preorbital part of maxilla	Narrow concavity	Narrow concavity	Long concavity	Short convexity
Mandible	Mandibular chin prominence	Absent	<i>D. claytoni</i> present <i>D. emryi</i> not present	Present	Usually present

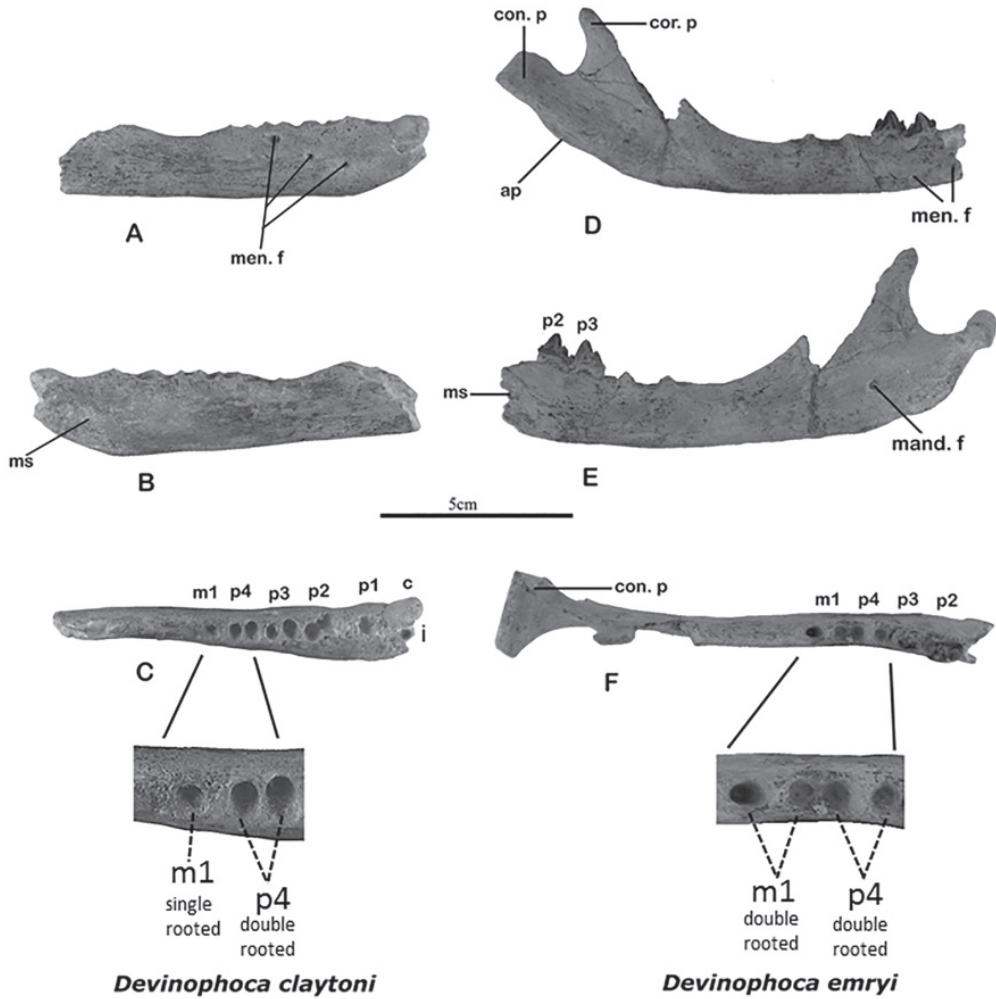


Fig. 2. Mandibles of *D. claytoni*: A — labial; B — lingual; C — occlusal views. *D. emryi*: D — labial; E — lingual, F — occlusal views. Abbreviations: ap — angular process; con. p — condyloid process; cor. p — coronoid process; men. f — mental foramina; ms — mandibular symphysis.

flat from the middle of the alveolus of p3 to the mandibular ramus, and swollen from the incisor to the middle of the alveolus of p3. On its labial side, the body of the mandible is thickened in the middle from the level of the anterior alveolus of p2 and the lingual side of this mandible is more swollen than the labial side. While the p1 and p3–m1 are oriented parallel to the axis of the mandibular body (similarly to all postcanine teeth in *D. emryi*), the p2 is oriented obliquely.

As opposed to *D. emryi*, the mental process is present, albeit not prominent, between p1 and p2. The maximal height of the mandible is at p2. The body of the mandible is straight, as opposed to the slightly curved mandibular body in *D. emryi*. The symphyseal part is thick and straight, similar to that in *D. emryi*. The symphysis reaches the anterior alveolus of p2, in contrast to *D. emryi* where it reaches the middle of the alveolus of p2. The posterior alveoli of the premolars are round shaped, as opposed to the oval shape in *D. emryi*.

The lower canine projects obliquely and its crown is flattened with age due to wear. The apex of c1 bears an oval wear facet that is directed anterolaterally. Diastemata between the teeth are absent, similar to *D. emryi*. Three mental foramina are present on the mandibular body, with the first located between the alveoli of p1 and p2, the second located between the

alveoli of p2 and p3 and the third located between the alveoli of p3 and p4 (fig. 2, A–C). The second and third mental foramina are located at the same level in a shallow groove in the middle of the mandibular body, while the first mental foramen is located slightly inferiorly in its own depression. The retromandibular space is shorter and more concave than in *D. emryi*. The portion of the existing mandibular ramus of *D. claytoni* is much thicker than the corresponding portion of *D. emryi*, suggesting that the rest of the missing ramus would also be thicker.

Comparisons with some representatives of the subfamily Cystophorinae

The first fossil record of the subfamily Cystophorinae included the description of postcranial bones only (Koretsky and Rahmat, 2013). Phylogenetic and morphological analyses of these pachyosteosclerotic bones helped erect a new genus (*Pachyphoca*) with two new species of extinct cystophorine seals from the middle Miocene (Middle Sarmatian, ~11.2–12.3 Ma) of the Northern Paratethys. No fossil cranial material or mandibles have ever been found for the subfamily Cystophorinae, necessitating the examination of a Recent cystophorine seal for this comparison to *D. claytoni*.

Cystophorine seals have obvious sexual dimorphism in cranial and postcranial elements, especially in the genus *Mirounga*. Elephant seals (*Mirounga*) and hooded seals (*Cystophora*) are extant sister taxa of the subfamily Cystophorinae (however, for an alternative view see Boessenecker and Churchill, 2016). Generally, *Cystophora cristata* (hooded seal) mandibles have a thin, square symphysis and premolar teeth aligned parallel to the mandibular axis. The *Cys. cristata* mandible differs from *D. claytoni* in the following characters: symphysis reaches only p1; mental process is located between p2 and p3; diastemata are present; alveoli of p2–m1 double rooted; alveoli of p4 are smaller than alveoli of m1 (fig. 3, D). The retromandibular space in males is more elongated than in females. The coronoid process in males is positioned lower than in females and ends at almost the same level as the condyloid process (as opposed to the other subfamilies). Females have a more developed angular process and a deeper, better outlined masseteric fossa than males.

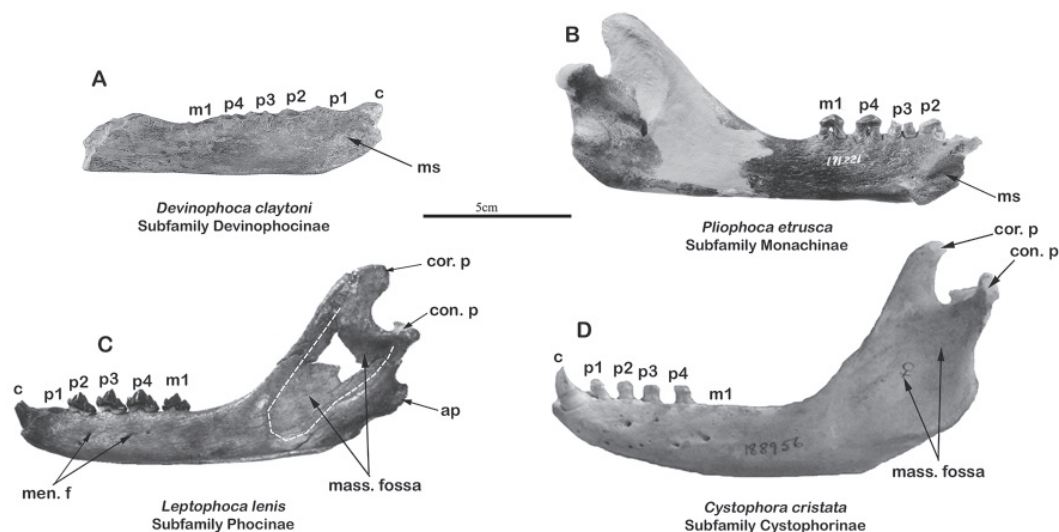


Fig. 3. Mandibles representing different subfamilies of Phocidae (true seals). A — left mandible in lingual view (SNMZ 25510, referred material) of *Devinophoca claytoni* (subfamily Devinophocinae). B — left mandible in lingual view of *Pliophoca etrusca* (subfamily Monachinae; National Museum of National History, Washington D.C., NMNH 171221). C — left mandible in labial view of *Leptophoca lenis* (subfamily Phocinae; Calvert Marine Museum, Maryland, CMM-V2021). D — left mandible in labial view of *Cystophora cristata* (subfamily Cystophorinae, National Museum of National History, Washington D.C., NMNH 188956, female). Abbreviations: ap — angular process; con. p — condyloid process; cor. p — coronoid process; mass. fossa — masseteric fossa; men. f — mental foramina; ms — mandibular symphysis.

Comparisons with some fossil representatives of the subfamily Monachinae

Similar to *D. claytoni*, the mandible of *Afrophoca libyca* (lower Miocene, ~19 Ma) has a mental prominence, the alveolar width of p4 is greater than that of m1, the alveolus of m1 is compressed craniocaudally and diastemata between teeth are absent. The craniocaudal compression of all posterior roots of the lower postcanine teeth is present in *D. claytoni* and the oldest known seal mandible (Koretsky and Domning, 2014: fig. 1), *Afrophoca libyca*. The *Af. libyca* mandible differs from *D. claytoni* in the following characters: a thick and deep mandibular body; the symphysis reaches the middle of the p2 alveoli; the entire postcanine tooth row is oriented parallel to the axis of the mandible, similar to *D. emryi*.

The mandible of *Pontophoca sarmatica* (middle Miocene, Middle Sarmatian, ~13.6–11.2 Ma; Koretsky and Grigorescu, 2002: fig. 1) has double rooted p3 and p4, similar to

Table 2. Mean (X) and range of measurements (mm) of number in sample (n) of the mandibles and lower dentition

Characters	Devinophoca			
	<i>D. emryi</i>		<i>D. claytoni</i>	
	n	X	Range	
Total length	1		131.5	–
Length of toothrow i1–1	1		53.4	55.2
Length of toothrow p1–p4	3	34.7	33.3–36.7	38.7
Length of toothrow p1–m1	3	45.3	44.4–46.8	44.9
Depth under m1	3	19.3	18.8–20.0	19.0
Depth under p2	2	20.2	20.0–20.4	19.7
Depth behind m1	3	16.4	15.9–16.7	18.4
Depth between p3–p4	3	17.5	16.7–17.9	19.5
Thickness of mandible under m1	3	8.5	8.3–8.7	9.4
Height of ramus	2	48.4	44.9–51.8	–
Length of condyle	3	21.7	20.5–23.8	–
Length of retromandibular space	3	12.6	9.7–14.2	19.0
Length of symphysis	1		23.0	21.2
Condylar height	3	29.0	21.7–36.0	–
i1	1		4.6	9.1
width	1		3.8	6.5
length				10.2
c				
width	1		8.9	7.6
length	4	6.2	4.8–6.9	4.2
p1				
width	4	5.0	4.8–5.1	5.9
length	3	9.4	9.0–9.6	10.6
p2				
width	3	5.4	4.8–5.9	6.9
length	3	11.0	10.0–13.0	9.1
p3				
width	3	5.7	5.2–6.3	7.1
length	4	10.8	9.6–12.7	9.2
p4				
width	4	5.2	4.2–6.1	6.6
length	3	11.3	10.5–12.3	4.4
m1				
width	3	4.0	3.5–4.4	5.4

D. claytoni. The *Pon. sarmatica* mandible differs from *D. claytoni* in the following characters: the postcanine tooth row is oriented parallel to the mandibular axis; diastemata between teeth are present; p4 is considerably larger than p3.

The *Properiptychus argentinus* mandible (middle Miocene, ~13.6–11.6 Ma; Muizon and Bond, 1982: fig. 3) has a flattened mandibular body low in height, pronounced symphyseal part and lacks diastemata, similar to *D. claytoni*. The *Pr. arentinus* mandible differs from *D. claytoni* in the following characters: oval-shaped alveoli; prominent mental process between p2 and p3; posterior edge of symphysis is between p2 and p3; postcanine teeth aligned parallel to mandibular axis; p4 larger than m1; double-rooted m1, with anterior root larger than posterior.

The *Acrophoca longirostris* (late Miocene; ~7.2–5.3 Ma; Muizon, 1981 a: pl. 7, figs 4, 5) mandible has double rooted p3 and p4, similar to *D. claytoni*. The mandibular body is low and flat. The *Ac. longirostris* mandible differs from *D. claytoni* in the following characters: double rooted m1; lack of mental process; elongated mandible; diastemata present.

The mandible of *Hadrokirus martini* (late Miocene; ~7.2–5.3 Ma; Amson and Muizon, 2014: fig. 8) has a short mandibular body. Similar to *D. claytoni*, the mandibular symphysis reaches the p2 alveolus, and p3 and p4 are both double rooted. The *Hadrokirus martini* mandible differs from *D. claytoni* in the following characters: extremely robust mandibular body; m1 is double rooted, in contrast to *D. claytoni* where m1 is single rooted.

The mandible of *Piscophoca pacifica* (late Miocene; ~7.2–5.3 Ma; Muizon 1981a: pl. 2, fig. 1; Walsh and Naish, 2002) is incomplete, missing the coronoid process, but is relatively robust, has a mandibular symphysis reaching p2, and the alveoli of p4 are larger than those of m1, similar to *D. claytoni*. The *Pis. pacifica* mandible differs from *D. claytoni* in the following characters: larger size; diastemata present; double rooted m1.

The *Homiphoca capensis* mandible (late Miocene–early Pliocene, ~7.0–3.2 Ma; Muizon and Bond, 1982; Koretsky and Ray, 2008: fig. 49) has wide and round alveoli, a prominent symphyseal part and no diastemata, similar to *D. claytoni*. The *H. capensis* mandible differs from *D. claytoni* in the following characters: tall mandibular body; prominent mental process located under the middle of p2; postcanine teeth aligned parallel to the mandibular axis; m1 larger than p4; double-rooted m1.

The *Callophoca obscura* mandible (early Pliocene, ~5.0–3.2 Ma; Koretsky and Ray, 2008: figs 28–29) has a thick symphysis with a weakly pronounced mental process, similar to *D. claytoni*. The *Cal. obscura* mandible differs from *D. claytoni* in the following characters: diastemata are present; the mental process is located between p2 and p3; the symphysis reaches the middle of p3; rounded symphysis; postcanine teeth are aligned oblique to the mandibular axis.

The mandible of *Pliophoca etrusca* (early Pliocene, ~5.0–3.2 Ma; Koretsky and Ray, 2008: figs 42–43) has a short mandibular body and a considerably high mandibular ramus. Similar to *D. claytoni*, diastemata are absent; the alveolus of m1 is smaller than that of p4; and m1 is double rooted. The *Pl. etrusca* mandible differs from *D. claytoni* in the following characters: mental process located between p2 and p3; postcanine teeth aligned oblique to the mandibular axis; anterior alveoli are oblique to the lingual side; symphysis reaches the anterior alveolus of p3 (fig. 3, B).

Comparisons with some fossil representatives of the subfamily Phocinae

Recently, Dewaele et al. (2017) declared that *Leptophoca lenis* (middle Miocene, ~16 Ma; Koretsky, 2001: fig. 42) is a junior synonym of *L. proxima*. We feel that more work needs to be done to support or dismiss this nomenclature change. Therefore, we will continue to use *L. lenis* in this paper. The discussion of transferring *L. lenis* into a new name is not in the scope of this study. We are examining the morphological characters of the *Leptophoca* mandible in comparison to the newly described *D. claytoni* mandibular

Table 3. Mandibular comparative diagnostic characters of representatvies of seals

Characters	Devinophocinae		Phocinae		Monachinae						Cystophorinae
	<i>Devinophoca claytoni</i>	<i>Devinophoca emryi</i>	<i>Leptophoca lenis</i>	<i>Praepusa vindobonensis</i>	<i>Afrophoca libyca</i>	<i>Cryptophoca maeotica</i>	<i>Piscophoca pacifica</i>	<i>Pliophoca etrusca</i>	<i>Gallophoca obscura</i>	<i>Acrophoca longirostris</i>	<i>Cystophora cristata</i>
Mandibular symphysis reaches anterior alveolus of p2	+	-	-	-	-	+	+	+	-	-	-
Symphyseal part thick and straight	+	+	-	-	+	+	-	+	-	+	-
Chin prominence present	+	-	-	+	+	+	+	-	-	+	+
Chin prominence located between 1-p2	+	-	-	-	-	-	-	-	-	-	-
Maximum height of mandibular body at p2	+	-	-	-	-	-	-	-	-	-	-
Diastema present	-	-	+	+	-	+	+	+	+	+	+
Alveoli of p4 larger than m1	+	+	+	+	+	+	+	-	-	-	-
Retromandibular space elongated	-	+	+	+	?	?	-	+	+	+	+
Number of incisors: 3/1	+	+	-	-	-	-	-	-	-	-	-
Roots of postcanine teeth (P, p2-P, p3) fused	-	-	+	-	-	-	-	-	-	-	+
Roots of P, p4:3	+	+	+	-	-	-	-	-	-	-	-
Crowns of postcanine teeth multicusped	+	+	+	+	+	?	?	+	+	+	-
Dimensions of postcanine teeth relative to longitudinal diameter of upper canine alveolus less than 60 % or sub-equal	+	+	+	+	?	+	?	-	-	?	-
Longitudinal diameter of upper canine alveolus compared with maximum width of infraorbital foramen sub-equal in size	+	+	-	+	?	-	?	-	-	?	-
Basal cingulum of postcanine teeth well developed	-	+	+	+	-	?	+	+	+	+	-
Additional cusps of premolars present	+	+	+	+	+	?	+	+	+	+	-
Premolars aligned parallel to axis of tooth-row	+/-	+	+	-	+	+	-	-	-	-	+
Upper incisors arranged in curved arcade	+	+	+	+	?	?	-	+	+	?	-
Third upper incisor larger than second	+	+	+	+	?	?	-	-	-	?	-

Note. + = character present; - = character absent/not well developed; ? = unknown.

material. *L. lenis* is one of the most primitive seals from the subfamily Phocinae, has a swollen and thick mandibular body, as opposed to *D. claytoni* where it is low and flat in the retromandibular region only (fig. 3, A, C). Similar to *D. emryi*, a mental process is absent. The *L. lenis* mandible differs from *D. claytoni* in the following characters: diastemata are present; all postcanine teeth are aligned parallel to the mandibular axis; symphyseal part is not pronounced (fig. 3, C).

The mandibular body of *Cryptophoca maeotica* (middle/late Miocene, ~13.6–11.2 Ma; Koretsky and Ray, 1994: fig. 1) is low, and its labial side is thickened in the middle from the level of the anterior alveolus of p2, similar to *D. claytoni*. The *Cr. maeotica* mandible differs from *D. claytoni* in the following characters: the postcanine tooth row is oriented parallel to the axis of the mandible, similar to *D. emryi*; the mental process is located between p3 and p4; the maximal height of the mandible is between the alveoli of p2 and p4.

In the *Praepusa vindobonensis* (middle Miocene, ~12.3–11.0 Ma, Antoniuk and Koretsky, 1984; Koretsky, 2001: fig. 23) mandible, the premolars are oriented obliquely to the axis of the tooth row, similar to p2 in *D. claytoni*, but opposite from other postcanine teeth which are oriented parallel to the mandibular axis. The *Pr. vindobonensis* m1 is double rooted, as opposed to the single rooted m1 in *D. claytoni*. The *Pr. vindobonensis* mandible also differs from *D. claytoni* in the following characters: the mental process is located between p3 and p4; diastemata are present, with the diastema between p4 and m1 being larger than that between p3 and p4.

Discussion and conclusions

Representatives from the three extant (Cystophorinae, Monachinae and Phocinae) and one extinct (Devinophocinae) phocid subfamilies were used to demonstrate comparative diagnostic mandibular characters of seals (table 2). The *Devinophoca claytoni* mandible has a mixture of characters from all four subfamilies (p2 double rooted; posterior alveoli larger than anterior; low mandibular body; alveoli of p4 larger than m1) as well as some unique characters (the tooth row from p3–m1 as well as p1 is oriented parallel to the axis of the body of the mandible and the canine and p2 are oriented obliquely; single rooted lower m1; three rooted upper M1). These results support our previous findings on the skull, mandible and teeth (Koretsky and Rahmat, 2015) as well as postcranial bones (Rahmat and Koretsky, 2016) of *D. emryi*, the sister taxon of *D. claytoni*.

The *D. claytoni* mandible has a similar dental formula as other Phocidae. Each seal subfamily has its own unique incisor formula with Phocinae having 10 incisors (I3/2; 6 upper and 4 lower), Monachinae (I2/2; 4 upper and 4 lower) and Devinophocinae (I3/1; 6 upper and 2 lower) having 8 incisors (with a different combination) and Cystophorinae having 6 incisors (I2/1; 4 upper and 2 lower). Thus, the two species of the subfamily Devinophocinae have three upper incisors (as in Phocinae, primitive condition) and one lower incisor (as in Cystophorinae, derived condition). The number of incisors is has long been used for classification of modern seals (Chapksii, 1955; 1974). The incisors formula, in addition to cranial morphology (which is severely limited due to the fragility of fossil seal skull remains), can be used to classify fossil seals also.

The skull of *D. claytoni* also has a three-rooted upper M1, suggesting that a lack of space in the oral cavity may be why the mandible only has a single-rooted lower m1, a rare phocid feature also observed in a few *Mirounga* (Boessenecker and Churchill, 2016). The skull of *D. claytoni* (Koretsky and Holec, 2002) and this new mandible demonstrate that no other phocid has a maxillary M1 with three cusps and three roots in a triangular arrangement.

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References

- Amson, E., Muizon, C. de. 2014. A new durophagous phocid (Mammalia: Carnivora) from the late Neogene of Peru and considerations on monachine seals phylogeny. *Journal of Systematic Palaeontology*, 12, 523–548.
- Antoniuk, A. A., Koretsky, I. A. 1984. A new seal species from the middle Sarmatian deposits of the Crimean district of Ukraine. *Vestnik Zoologii*, 4, 26–31.
- Ärnason, U., Gullberg, A., Janke, A., Kullberg, M., Lehman, N., Petrov, E. A., Väinölä, R. 2006. Pinniped Phylogeny and a new Hypothesis for their Origin and Dispersal. *Molecular Phylogenetic and Evolution*, 41, 345–354.
- Barnes, L. G., Hirota, K. 1994. Miocene Pinnipeds of the Otariid subfamily Allodesminae in The North Pacific Ocean: Systematics and Relationships. In: Barnes, L. G., Hasegawa, Y., Inuzuka, N., eds. *The Island Arc, Special Issue, Evolution and Biogeography of Fossil Marine Vertebrates in the Pacific Realm. Collected Papers from A Symposium Dedicated to the Memory of Arthur Remington Kellogg in the Year of the 100th Anniversary of his Birth-1992*. Proceedings of the 29th International Geological Congress. Kyoto, Japan, 329–360.

- Berta, A., Sumich, J. L. 1999. *Marine Mammals: Evolutionary Biology*. Academic Press, San Diego, 1–494.
- Berta, A., Wyss, A. R. 1994. Pinniped Phylogeny. In: Berta, A., Deméré, T. A., eds. *Contributions in Marine Mammal Paleontology Honoring Frank C. Whitmore, Jr.* Proceedings of the San Diego Society of Natural History, 29, 3356.
- Berta, A., Kienle, S., Bianucci, G., Sorbi, S. 2015. A reevaluation of *Pliophoca etrusca* (Pinnipedia, Phocidae) from the Pliocene of Italy: phylogenetic and biogeographic implications. *Journal of Vertebrate Paleontology*, 35. DOI 10.1080/02724634.2014.889144.
- Bininda-Emonds, O. R. P., Russell, A. P. 1996. A morphological perspective on the phylogenetic relationships of the extant phocid seals (Mammalia: Carnivora: Phocidae). *Bonner zoologische Monographien*, 41, 1–256.
- Boessenecker, R. W., Churchill, M. 2016. The origin of elephant seals: implications of a fragmentary late Pliocene seal (Phocidae: Miroungini) from New Zealand. *New Zealand Journal of Geology and Geophysics*. DOI 10.1080/00288306.2016.1199437.
- Bowman, R. I. 1961. *Morphological Differentiation and Adaptation in the Galápagos Finches*. Berkeley University of California Press. 1–326.
- Burns, J. J., Fay, F. H. 1970. Comparative morphology of the skull of the Ribbon seal, *Histriophoca fasciata*, with remarks on systematics of Phocidae. *Journal of Zoology* (London), 161, 363–394.
- Chapksii, K. K. 1955. An attempt at revision of the systematics and diagnostics of seals of the subfamily Phocinae. *Trudy Zoologich. Inst. Akademii Nauk SSSR*, 17, 160–199 [In Russian]. (English translation by Jeletzky, T. F., *Fisheries Research Board of Canada, Translational Series*, 114, 1–57, 1957).
- Chapksii, K. K. 1974. In defense of classical taxonomy of the seals of the family Phocidae. *Trudy Zool. Inst. Acad. Sci. USSR*, 53, 282334 [In Russian].
- Churchill, M., Clementz, M. T., Kohno, N. 2014. Predictive equations for the estimation of body size in seals and sea lions (Carnivora: Pinnipedia). *Journal of Anatomy*, 225, 232–245.
- Dewaele, L., Lambert, O., Louwyse, S. 2017. On *Prophoca* and *Leptophoca* (Pinnipedia, Phocidae) from the Miocene of the North Atlantic realm: redescription, phylogenetic affinities and paleobiogeographic implications. *PeerJ*, 5, e3024. DOI 10.7717/peerj.3024.
- Dewaele, L., Mauricio C. P., Meyvisch, P., Louwyse, S. 2018. Diversity of late Neogene Monachinae (Carnivora, Phocidae) from the North Atlantic, with the description of two new species. *Royal Society of Open Science*. 172437; DOI 10.1098/rsos.172437.
- Fejfar, O., Sabol, M. 2009. Middle Miocene Plesiodimylus from the Devínska Nová Ves-Fissures site (western Slovakia). *Bulletin of Geosciences*, 84 (4), 611–624.
- Flynn, J. J., Finarelli, J. A., Zehr, S., Hsu, J., Nedbal, A. 2005. Molecular Phylogeny of the Carnivora (Mammalia): Assessing the Impact of Increased Sampling on Resolving Enigmatic Relationships. *Systematic Biology*, 54 (2), 317–337.
- Fulton, T. L., Strobeck, C. 2006. Molecular phylogeny of the Arctoidea (Carnivora): effect of missing data on supertree and supermatrix analyses of multiple gene data sets. *Mol Phylogenet Evol.*, 41, 165–181.
- Ge, D., Wen, Z., Xia, L., Zhang, Z., Erbajeva, M., Huang, C., Yang, Q. 2013. Evolutionary History of Lagomorphs in Response to Global Environmental Change. *PLoS ONE*, 8 (4). DOI 10.1371/journal.pone.0059668.
- Goldin, P. E., Pilipenko, D. A. 2012. *New findings of seal Monachopsis pontica from Neogene of Kerch Peninsula*. In: Lopatin, A. V., Parkhaev, P. Yu., Rozanov, A. Yu., eds. *Modern paleontology: classical and newest methods*. The Ninth All-Russian Scientific School for Young Scientists in Paleontology (October 1–3, 2012. Borissiak Paleontological Institute of the Russian Academy of Sciences, Moscow): book of abstracts, 17 [In Russian].
- Holec, P., Klembara, J., Meszároš, S. 1987. Discovery of new fauna of marine and terrestrial vertebrates in Devínska Nová Ves. *Geologica Carpathica*, 38, 349356.
- Holec, P., Sabol, M. 1996. The Tertiary vertebrates from Devínska Kobyla. *Miner. Slov.*, 28, 519–522 [In Slovak].
- Holec, P., Klembara, J., Meszároš, S. 1997. Fossils of the Devínska Kobyla hill. In: Feráková, V., ed. *Flora of the Devínska Kobyla hill*, 1–639. APOP-Edition, Bratislava [In Slovak].
- King, J. E. 1983. *Seals of the World: Second Edition*, British Museum (Natural History), Comstock Publishing Associates, Ithaca, New York, 1–240.
- Koretsky, I. A., Ray, C. E. 1994. *Cryptophoca*, new genus for *Phoca maeotica* (Mammalia: Pinnipedia: Phocinae) from Upper Micoene deposits in the Northern Black Sea region. *Proceedings of the Biological Society of Washington*, 107, 17–26.
- Koretsky, I. A. 2001. Morphology and Systematics of Miocene Phocinae (Mammalia: Carnivora) from Paratethys and the North Atlantic Region. *Geology of Hungary*. Budapest, 54, 1–109.
- Koretsky, I. A., Grigorescu, D. 2002. The Fossil Monk Seal *Pontophoca sarmatica* (Alekseev) (Mammalia: Phocidae: Monachinae) from the Miocene of Eastern Europe. *Smithsonian Contributions to Paleobiology*, 93, 149–162.
- Koretsky, I. A., Holec, P. 2002. A primitive seal (Mammalia: Phocidae) from the Early Middle Miocene of Central Paratethys. *Smithsonian Contributions to Paleobiology*, 93, 163–178.
- Koretsky, I. A., Barnes, L. G. 2006. Pinniped evolutionary history and paleogeography. In: Csiki, Z., ed. *Mesozoic and Cenozoic vertebrates and paleoenvironments*. Tribute to the career of Professor Dan Grigorescu-Bucharest, ArsDocendi, 143–153.

- Koretsky, I. A., Ray, C. E. 2008. Phocidae of the Pliocene of eastern USA. *Virginia Museum of Natural History Special Publication*, 14, 81–140.
- Koretsky, I. A., Ray, C. E., Peters, N. 2012. Miocene seals of the Netherlands, Part I: A New Species of *Leptophoca* (Carnivora, Phocidae, Phocinae) from Both Sides of the North Atlantic Ocean. *DEINSEA*, 15. *Annual of the Natural History Museum Rotterdam*, the Netherlands, 1–12.
- Koretsky, I. A., Rahmat, S. J. 2013. First Record of fossil Cystophorinae (Carnivora, Phocidae): Middle Miocene seals from the Northern Paratethys. *Rivista Italiana di Paleontologia e Stratigrafia*, 119 (3), 325–350.
- Koretsky, I. A., Domning, D. P. 2014. One of the oldest seals (Carnivora, Phocidae) from the Old World. *Journal of Vertebrate Paleontology*, 34 (1), 224–229
- Koretsky, I. A., Rahmat, S. J. 2015. A New Species of the Subfamily Devinophocinae (Carnivora: Phocidae) from the Central Paratethys. *Rivista Italiana di Paleontologia e Stratigrafia*, 121 (1), 1–17.
- Koretsky, I. A., Barnes, L. G., Rahmat, S. J. 2016. Re-evaluation of morphological characters questions current views of pinniped origins. *Vestnik Zoologii*, 50 (4), 327–354.
- Losos, J. B. 2011. *Lizards in an evolutionary tree: ecology and adaptive radiation of anoles*. University of California Press, 1–528.
- McKenna, M. C., Bell, S. K. 1997. *Classification of Mammals above the Species Level*. Columbia University Press, New York, 1–631.
- Mitchell, E. D. 1968. The Mio-Pliocene pinniped. *Imagotaria Journal of the Fisheries Research Board of Canada*, 25 (9), 1843–1900.
- Muizon, C. de. 1981 a. Les vertebres fossiles de la Formation Pisco (Perou). Premiere parti: Deux nouveaux Monachina (Phocidae, Mammalia) du Pliocene de Sud-Sacaco. *Recherche sur les grandes civilisations Memoire*, 6, 1–150.
- Muizon, C. de. 1981 b. Premier signalement de Monachinae (Phocidae: Mammalia) dans le Sahélien (Miocène Supérieure) d'Oran (Algérie). *Palaeovertebrata*, 11, 181–194.
- Muizon, C. de. 1992. Paläontologie. In: Duguy, R., Robineau, D., eds. *Handbuch der Säugetiere Europas*, Band 6: Meeressäuger. Teil II: Robben-Pinnipedia, 34–41. AULA-Verlag, Wiesbaden.
- Muizon, C. de, Bond, M. 1982. Le Phocidae (Mammalia) de la Formation Parana (Entre Rios, Argentine). *Bulletin de Musee de Histoire Naturelle, Paris, 4th ser, section C*, 4 (3–4), 165–207.
- Nyakatura, K., Bininda-Emonds, O. R. P. 2012. Updating the evolutionary history of Carnivora (Mammalia): a new species-level supertree complete with divergence time estimates. *BMC Biology*. 10:12. DOI 10.1186/1741-7007-10-12.
- Rahmat, S. J., Koretsky, I. A. 2016. First record of postcranial bones in *Devinophoca emryi* (Carnivora, Phocidae, Devinophocinae). *Vestnik Zoologii*, 50, 1, 71–84.
- Repenning, C. A., Tedford, R. H. 1977. Otarioid seals of the Neogene. *Geological Survey Professional Paper*, 992, 1–93.
- Scheel, D. M., Slater, G. J., Kolokotronis, S. O., Potter, C. W., Rotstein, D. S., Tsangaras, K., Greenwood, A. D., Helgen, K. M. 2014. Biogeography and taxonomy of extinct and endangered monk seals illuminated by ancient DNA and skull morphology. *ZooKeys*, 14 (409), 1–33.
- Schultz, O. 2004. A Triggerfish (Osteichthyes: Balistidae: *Balistes*) from the Badenian (Middle Miocene) of the Vienna and the Styrian Basin (Central Paratethys). *Annalen des Naturhistorischen Museums in Wien*, 106 A, 345–369.
- Sokolov, V. E. 1979. *Systematics of Mammals: Cetacea, Pinnipedia, Carnivora, Tubulidentia, Tylopoda, Perissodactyla*. Higher School, Moscow, 1–718.
- Wagreich, M., Hohenegger, J., Ćorić, S. 2014. Base and New Definition of the Lower Badenian and the Age of the Badenian Stratotype (Middle Miocene, Central Paratethys). In: Rocha, R., Pais, J., Kullberg, J., Finney, S., eds. *STRATI 2013*. Springer Geology. Springer, Cham.
- Walsh, S., Naish, D. 2002. Fossil seals from late Neogene deposits in South America: A new pinniped (Carnivora, Mammalia) assemblage from Chile. *Palaeontology*, 45 (4), 821–842.
- Wozencraft, C. 1989. The phylogeny of the Recent Carnivora. In: Gittleman, J. L., ed. *Carnivore Behavior, Ecology, and Evolution*. New York, NY, 495–535.
- Wyss, A. R. 1987. The walrus auditory region and monophyly of pinnipeds. *American Museum Novitates*, 2871, 1–31.
- Wyss, A. R. 1994. The evolution of body size in phocids: some ontogenetic and phylogenetic observations. In: Berta, A., Deméré, T. A., eds. *Contributions in Marine Mammal Paleontology Honoring Frank C. Whitmore, Jr. Proceedings of the San Diego Society of Natural History*, 29, 69–77.
- Yonezawa, T., Kohno, N., Hasegawa, M. 2009. The monophyletic origin of sea lions and fur seals (Carnivora: Otariidae) in the Southern Hemisphere. *Gene*, 441, 89–99.

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